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THE
AMERICAN NATURALIST

VOL. XLII June, 1908 No. 498

THE ANCESTRY OF THE CAUDATE AMPHIBIA

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THE phylogeny of the group of vertebrates commonly called amphibians or batrachians has been, and still is to some extent, among the most obscure of the problems connected with the descent of animals. So far as I am aware there have been but few statements as to the possible ancestry of the Amphibia and no attempt has been made to set forth in detail the series of structures through which the animals have passed from the beginning of their line to the present. During the course of an extensive investigation on the extinct Amphibia of North America, the writer has reached some interesting conclusions in regard to the ancestry of at least one group of the modern Amphibia and these conclusions are here set forth in detail. Some of the facts offered in support of these conclusions have been given in other connections.

So far as at present known, the first trace of vertebrate life on earth is that of fishes in Ordovician rocks in Colorado and in two places in Wyoming, *i. e.,* the Black Hills and the Big Horn Mountains. In the Devonian, if the impressions from the Catskill are properly interpreted, the fishes had given rise to a quadrupedal type of animals which are usually known as the Amphibia. Only impressions of footprints in the sandstone are known, but these are quite instructive. There are no traces of the bones

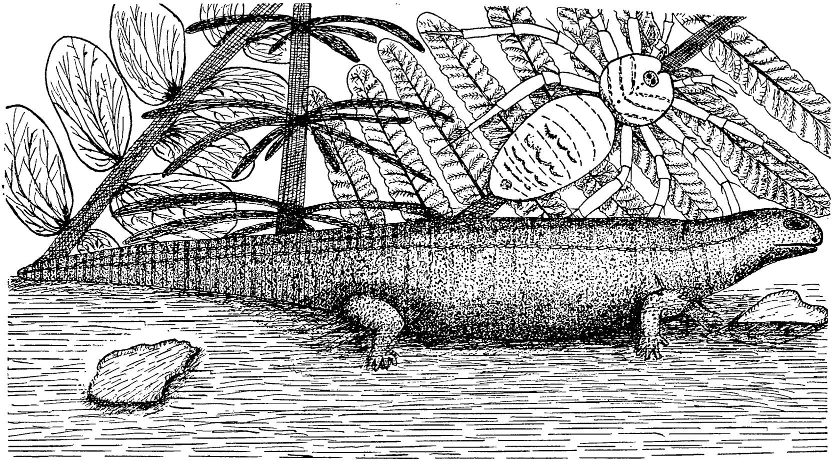

Fig. 1. Restoration of *Micrerpeton caudatum* Moodie from the Coal Measures of Illinois. Length of form, 49 mm. Spider is a composite restoration and is based on actual specimens and on the results of Roemer, Scudder, Beecher and Melander. × $2\frac{1}{3}$.

of these quadrupeds known in rocks of Devonian or of Mississippian age, although Lohest (1) some years ago called attention to some remains which he thought were amphibian from the Devonian rocks of France. Thevenin has recently cast doubt upon this interpretation by Lohest (2) and the figures as given by Lohest would seem not to be amphibian, but fish remains.

In rocks of the lower part of the Pennsylvanian occur, in North America, the first evidences of the bones of quadrupeds. The Amphibia show, even thus early, that their line had divided into three and possibly four distinct groups which are usually known as the Branchiosauria, the Microsauria, the Aistopoda and the Stereospondyli. The presence of the last group is indicated by the two vertebræ from the Carboniferous of Nova Scotia named by Professor Marsh *Eosaurus canadensis* and also by certain fragments of large ribs and large skulls from the coal beds of Ohio. The Temnospondyli did not make their appearance until the latter part of the Pennsylvanian, when their remains are found in Carboniferous rocks of Kansas, Illinois and Pennsylvania.

The Stereospondyli and the Temnospondyli are specialized side branches of the amphibian or reptilian stem and will not concern us further here. The Aistopoda are regarded by the writer at present as being specialized microsaurians. This would not favor the view of Wiedersheim as to the descent of the Cœcilians. This point needs further investigation and will be discussed elsewhere. The Microsauria Dr. Gadow has placed in the subclass Proreptiliæ and, in the opinion of the writer, his classification represents the correct facts, but further discussion will be postponed. The group to which the reader's attention is here invited is the one usually known as the Branchiosauria, representatives of which are found only in Western Europe and in North America, where a single specimen is known from Illinois. The group is a very small one both as to the size of the individual members and as to the number of species.

The Branchiosauria are distinguished from all of the other Amphibia-like vertebrates by the presence of short, heavy, straight ribs. The Microsauria always have long, thin, curved ribs. The Aistopoda usually are destitute of ribs or when present they are curved and slight. In conversation recently with Dr. Gadow he made the interesting suggestion that the characters presented by the ribs might be used as a basis on which to separate the group heretofore known as Stegocephala into two main divisions. One of the divisions would be the true Amphibia with the Branchiosauria as the representative order among the early forms, in which case the term Branchiosauria would be a misnomer, and the other Stegocephala would be included under some such name as the Pro-

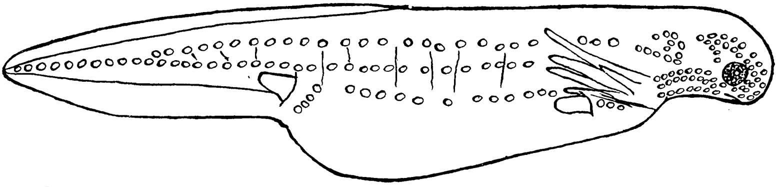

FIG. 2. Outline of a Larva of *Necturus*, showing the arrangement of the lateral line systems. After Platt.

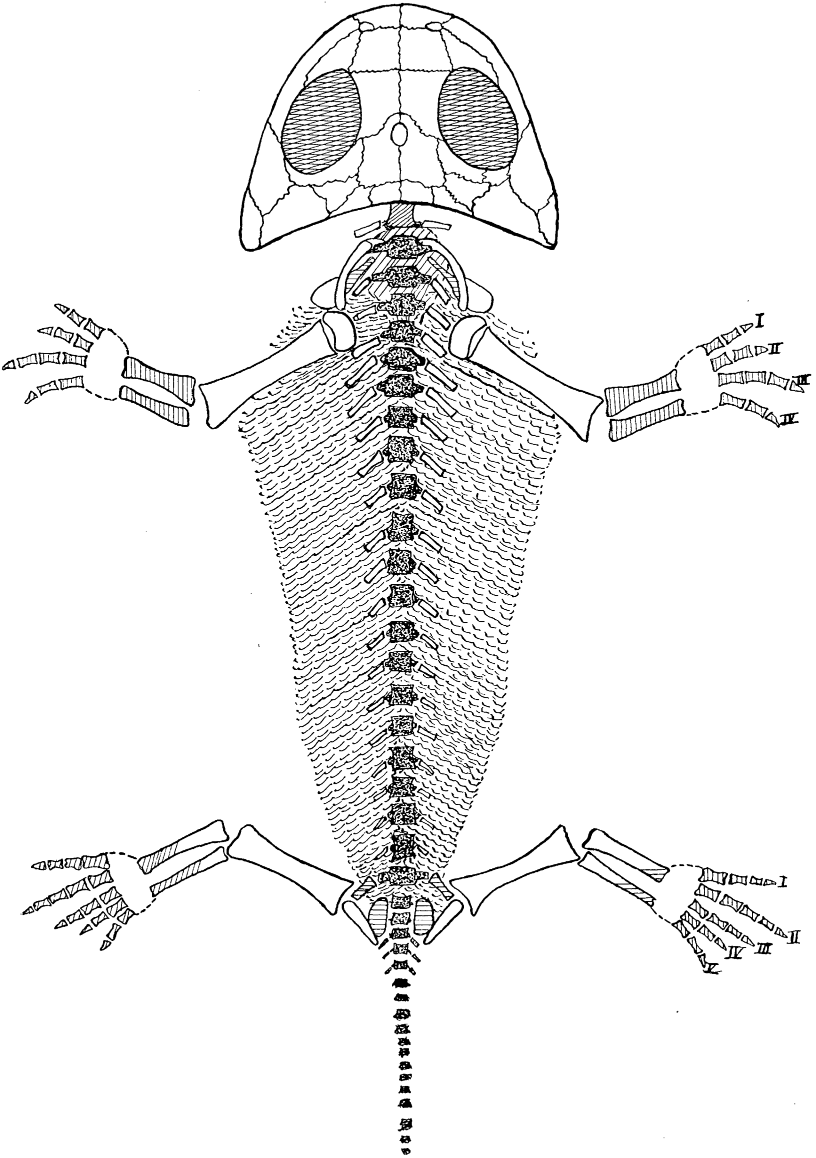

FIG. 3. Restoration of the Skeleton of *Micrerpeton caudatum* Moodie. The feet are conjectural and are based on the studies of Credner. The broad ventral armature is well developed in this form. × 3½.

reptilia or would be distributed among the reptiles proper. The former group is characterized by the short straight ribs borne on stout transverse processes and the latter group is characterized by the long curved ribs borne intercentrally. There seem to be some difficulties in this classification, but it is hoped that they may be cleared up by future investigation.

The Branchiosauria, as has been several times suggested by various authors, represent the ancestral forms of at least the tailed division of the Amphibia. A suggestion as to the ancestry of the tailless forms will be given elsewhere. The conclusion that the Branchiosauria are the direct ancestral forms to the modern Caudata is based on several characters. These characters are: the structure of the skull, the structure and form of the vertebræ and ribs, the number of digits, the arrangement of the phalangeal elements, the characters of the pectoral and pelvic girdles, the character of the lateral line system, the structure and form of the long bones and finally the shape of the body; all of which will be discussed below.

It has been suggested on embryological grounds that the Amphibia are a degenerate group (3) and this is borne out, in so far as the Caudata are concerned, by a study of the cranium of the early and recent forms as well as by other structures. The cranium of the Branchiosauria is almost identical in structure with that of the Microsauria and it exhibits a completely roofed-over skull with only five openings, namely, those for the orbits, the nostrils and the pineal opening.

The elements forming the roof of the skull are quite constant in the Branchiosauria and also in the Microsauria and they differ only in position and relations. Practically the same elements form the skull roof in the two groups, but the forms differ in other important respects. In the skull of the Branchiosauria we find in the median line a row of elements in pairs, which extend the entire length of the skull. These are (beginning anteriorly): the premaxillæ, the nasals, the frontals, the parietals and the supraoccipitals. On the side of these elements lie others which vary in their position to some extent; the median elements are fixed and not so likely to

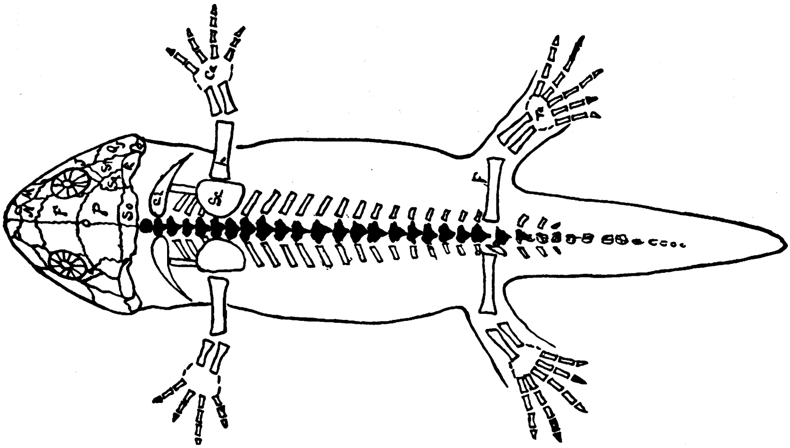

FIG. 4. Restoration with Outline of the *Branchiosaurus fayoli* Thevenin based on the figures given by Thevenin. The last phalanx in digit I of the hand is conjectural and the last two on digit II and the last one on digit IV of the foot are conjectural. From the Upper Carboniferous of France. × 2.

vary. Anterior to the orbit there are the prefrontal, the lachrymal, the maxilla, and lateral to the orbit lies the jugal. Posterior to the orbit lie the postorbital, the postfrontal, the squamosal, the supratemporal, the opiotic, and on the postero-lateral border of the skull lie the quadrato-jugal and quadrate.

In the skull of the modern Caudata we find an arrangement of the elements which is quite similar to that described for the Branchiosauria. In the skull of Megalobatrachus (Fig. 10), for instance, we find the following

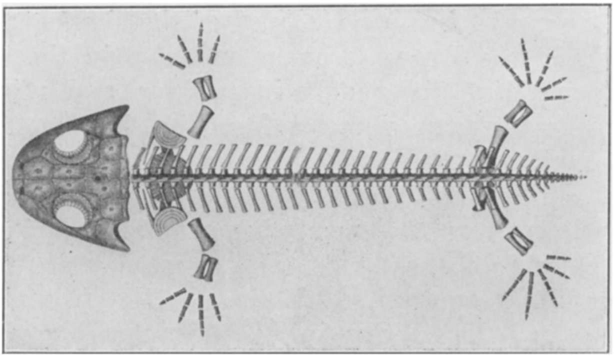

FIG. 5. Restoration of *Branchiosaurus amblystomus* Cred. from the Permian of Saxony. After Credner.

bones paired in the median line: the premaxillæ, the nasals, the frontals, the parietals, and on the posterior end of the skull occur the exoccipitals. In this series it is clear that the supraoccipital elements have disappeared. Lateral to the median paired row there are the maxilla, the prefrontal, the squamosal, and in allied forms the jugal, quadratojugal and quadrate. The epiotic is wanting in all skulls of modern amphibians except some coccidians and the elements are not so firmly united as in the skull of the Branchiosauria. The skull of the Caudata exhibits a weaker, more degenerate condition, than is found among the early forms. The lower surface of the skull is practically the same in the two groups, especially in the possession of a large parasphenoid. Teeth on the palate bones are lacking, for the most part, in the modern forms, which is another evidence of degeneracy.

If the structure of the vertebræ is now examined it will be seen that in this particular there is close affinity between the modern Caudata and the Paleozoic Branchiosauria. The vertebræ of the modern Caudata are amphicœlous and opisthocœlous, with the notochord rarely persistent and with the transverse processes springing off boldly from the body of the centrum. Similar conditions are observed in the Branchiosauria where the vertebræ, so far as they are known, are amphicœlous and the transverse process is unusually strong with the notochord probably persistent. The transverse processes give support to the short, heavy, stout ribs which lay in the flesh and made acute angles posteriorly with the vertebral column. The ribs in the Branchiosauria and in the later Caudata are indistinguishable so far as form is concerned. The point of difference is that in the modern forms the ribs are usually weaker posteriorly and are, for the most part, confined to the presacral region of the body. This is another instance in which the Caudata show their degenerate structure. On the basis of the ribs alone the Branchiosauria may well be separated from the Microsauria and from all other of the so-called Stegocephala, and would be considered as the true Amphibia,

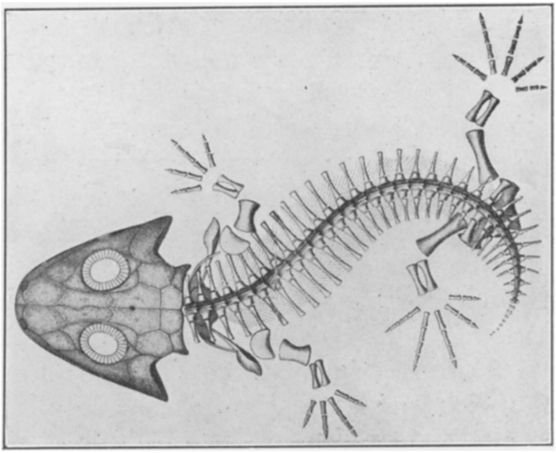

FIG. 6. Restoration of *Melanerpeton* from the Permian of Saxony. After Credner.

while all other forms would be excluded from this class and would have to be placed among the Reptilia, where they probably belong; whether they are to be considered as a subclass of the Reptilia or not, does not concern us here.

In the forelimb there are never more than four digits either in the Paleozoic Branchiosauria nor in the later Caudata. So far as I am aware, there is no paleontological evidence to show that there ever were more than four digits in the hand of the caudate Amphibia and in this discussion the first digit will be considered as No. I., the second digit as No. II. and so on. Fritsch, it is true, has figured five digits in the hand of *Branchiosaurus salamandroides* Fr. (Fig. 7), from the Permian of Bohemia, (4) but in giving us a glimpse into the material on which his restoration is based there are only four digits preserved in the hand, although Fritsch says the first had been lost. I doubt if there ever were more than four, and the digits in Fritsch's specimen were all preserved. In all of the Permian forms from Saxony Credner has figured four digits in the hand (Figs. 5–6).

The specimens recently described by Thevenin from the Upper Carboniferous of France (5) show only four digits in the hand. In Fig. 4 a restoration of the *Branchiosaurus fayoli* Thevenin has been attempted. The reconstruction is based on the figures as given by Thevenin. Only one phalanx is restored and that is the distal one of the first digit. All of the rest were preserved. In the Wealden of Belgium the *Hylæobatrachus croyii* Dollo (Fig. 8) exhibits but four digits in the hand. In *Andrias scheuchzeri* Tschudi (Fig. 9) from the Miocene of Switzerland, there are but four digits in the hand, and in all of the modern caudate forms, so far as I am aware, there are but four digits and the phalangeal formula for all, both in Paleozoic and in later forms, is universally 3-3-4-3.

In the foot the Branchiosauria show the same agreement with the modern Caudata. There are always five digits and they usually have the phalangeal formula 4-5-4-3-3. Neither the carpus nor the tarsus is fully ossified in the Branchiosauria or in the later Caudata, although the carpus and tarsus are partly osseous in the Amblystomatidæ.

The pectoral girdle of the Branchiosauria consists usually of four elements, three paired and one unpaired. These are: the single interclavicle, the clavicles, the coracoids (cleithra?) and the scapulæ. Among the modern

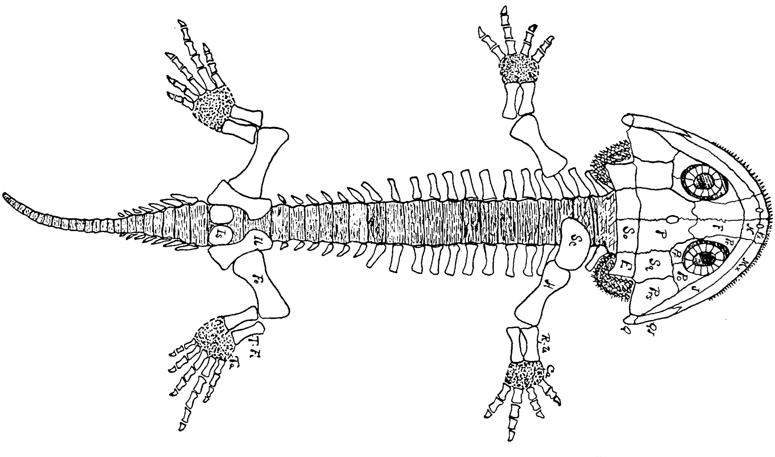

FIG. 7. Restoration of *Branchiosaurus salamandroides* Fr. from the Permian of Bohemia. Modified after Fritsch.

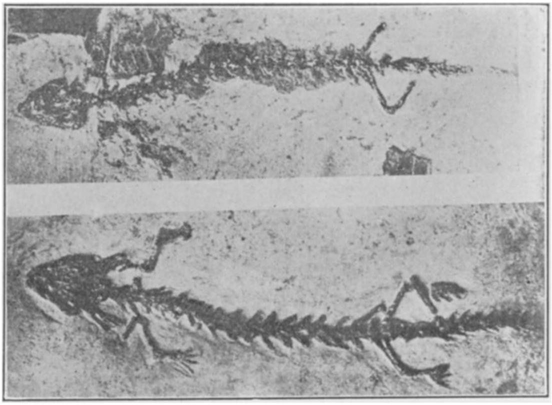

FIG. 8. *Hylæobatrachus croyii* Dollo from the Wealden of Bernissart. After Dollo.

caudate forms as well as among the Miocene forms all of the elements with the exception of the scapulæ have become cartilaginous, so that there remains in the modern caudate amphibians only a bony scapula. This seems to be the case in the Wealden Hylæobatrachus, but the single specimen is not well enough preserved to furnish definite information on this point. The pelvic girdle has, apparently, undergone no change in the evolution of the Caudata. The pubis is never ossified in either the Branchiosauria or in the latter Caudata and the ischium is usually plate-like, while the ilium is more or less rounded. The sacral rib, of which there is never more than one pair, is usually well developed.

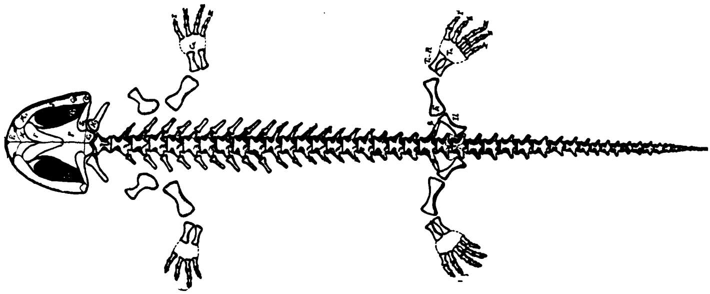

FIG. 9. Restoration of *Andrias scheuchzeri* Tschudi based on the drawings published by von Meyer in "Fauna der Vorwelt." × ¼.

In an essay now in press on "The Lateral Line Organs in Extinct Amphibia" the writer has called especial attention to the character of the lateral line organs as they are preserved in the single specimen of a branchiosaurian, Micrerpeton, from the Coal Measures of Illinois. A restoration of this form has been attempted in Fig. 1. The animal, as preserved, measures only 49 millimeters. It is apparently an adult, as there are no evidences of branchiæ and the limb bones are well formed. The spider shown in the restoration is a composite and is based partly on actual specimens partly on the results of Roemer, Beecher, Scudder and Melander. The body of the spider which was used as a model was about a half an inch in length. The particular characters in the amphibian which deserve mention now are the two lines representing the lateral line organs. There is seen a median lateral line which starts at the tip of the tail and runs forward. The other begins somewhat anteriorly and springs boldly from the median lateral line at a distance of a few millimeters from the tip of the tail. These lines represent rows of pigmented scales which show on the

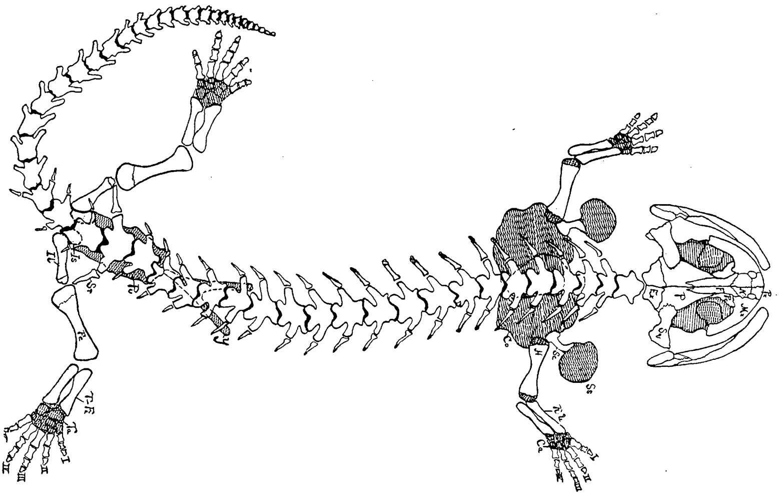

FIG. 10. The Skeleton of *Megalobatrachus japonicus* ——. After Osawa.

specimen as dark lines. The sense organs were undoubtedly located beneath these specialized scales, much as the lateral line organs are protected in some of the fishes. In Necturus (Fig. 2) the arrangement of the lateral line organs is almost identical with what has just been described for Micrerpeton. I have suggested elsewhere that this similarity in the lateral line organs of these two forms may be indicative of relationship between the groups to which these forms belong. There is no reason why the type of lateral line should not have been preserved in the amphibians, since we know that in some of the fishes certain types of peculiar lateral line structure have persisted for nearly as great a length of time.

In the structure of the limb bones and ribs the Branchiosauria are much like the modern Amphibia in that the bones are formed almost entirely of perichondrium. There are never any bony epiphyses in any of the Amphibia. In some of the toads Parsons has seen the cartilaginous epiphyses calcified, but they are never osseous. The endochondrium is not at all or but slightly developed in the Amphibia, and in the fossilized bones this condition causes a concavity at the ends. In the Microsauria the endochondrium is more fully formed, although there are some in which the ends of the limb bones are nearly flat.

The form of the body in the Branchiosauria is strikingly salamandrine, as may be seen by referring to figures 1 and 4. In Micrerpeton the tail is quite long and almost equals the length of the presacral region. In the *Branchiosaurus fayoli* Thevenin (Fig. 4), the tail is shorter but the form is much the same. The body of the Branchiosaurus (Fig. 4) is more stout than that of the Micrerpeton (Fig. 3) and the ribs are longer.

In summing up all of the characters as presented by the Caudata and the Branchiosauria it seems most probable that the Caudata are but degenerate Branchiosaurians and the changes which have taken place in the skeleton are mostly brought about by the loss of certain parts.

SUMMARY

1. The Stegocephala will probably have to be divided into two groups, one of which will be considered as Amphibia and the members of the other group will have to be placed among the Reptilia but can not all be placed under any single head since they represent divergent types and must be placed in with the reptilian groups to which they have probably given origin.

2. The Branchiosauria are the ancestral forms of at least the caudate Amphibia. The Branchiosauria are first known in the Pennsylvanian of North America and they present characters which separate them clearly from all other groups of the so-called Stegocephala.

3. The characters which the Branchiosauria have in common with the Caudata are: short, straight ribs; stout transverse processes springing from the body of the vertebra; practically the same number of presacral vertebræ; the same skull structure; the degenerate character of the pectoral girdle and the close correspondence of the pelvic girdle; the same number of the digits and the same phalangeal formula in the Branchiosauria and Caudata; the similar characters presented by the lateral line system; the structure of the long bones and the shape of the body.

4. There can be but little doubt that the Caudata are the direct descendants of the Branchiosauria, of which they are but degenerate forms.

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